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Published in:

Marine Technology Society Journal

DOI:

[10.4031/MTSJ.51.5.8](https://doi.org/10.4031/MTSJ.51.5.8)

Publication date:

2017

Citation for published version (APA):

Liao, J. C., & Akanyeti, O. (2017). Fish Swimming in a Kármán Vortex Street: Kinematics, Sensory Biology and Energetics. *Marine Technology Society Journal*, 51(5), 48-55. <https://doi.org/10.4031/MTSJ.51.5.8>

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**FISH SWIMMING IN A KÁRMÁN VORTEX STREET: KINEMATICS, SENSORY
BIOLOGY AND ENERGETICS**

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Abstract

Fishes often live in environments characterized by complex flows. To study the mechanisms of how fishes interact with unsteady flows, the periodic shedding of vortices behind cylinders has been employed to great effect. In particular, fishes that hold station in a vortex street (i.e. Kármán gaiting) show swimming kinematics that are distinct from their patterns of motion during freestream swimming in uniform flows, although both behaviors can be modelled as an undulatory body wave. Kármán gait kinematics are largely preserved across flow velocities. Larger fish have a shorter body wavelength and slower body wave speed than smaller fish, in contrast to freestream swimming where body wavelength and wave speed increases with size. The opportunity for Kármán gaiting only occurs under specific conditions of flow velocity and depends on the length of the fish; this is reflected in the highest probability of Kármán gaiting at intermediate flow velocities. Fish typically Kármán gait in a region of the cylinder wake where the velocity deficit is about 40% of the nominal flow. The lateral line plays a role in tuning the kinematics of the Kármán gait, since blocking it leads to aberrant kinematics. Vision allows fish to maintain a consistent position relative to the cylinder. In the dark, fish do not show the same preference to hold station behind a cylinder though Kármán gait kinematics are the same. When oxygen consumption level is measured, it reveals that Kármán gaiting represents about half of the cost of swimming in the freestream.

Introduction

Understanding how fishes swim in unsteady flows has attracted attention from many disciplines, ranging from biologists interested in fish ecology to engineers working on the

principles of efficient propulsion¹⁻⁵. Because the hydrodynamics of a cylinder wake is well-characterized⁶, examining how fish interact with cylinder vortices has provided a tractable way to begin to understand fish-fluid interactions under complex, yet predictable flow conditions⁷⁻⁹. This is because the relationships between flow velocity, cylinder diameter, and vortex shedding frequency are already known. Flow moving past the cylinder creates vortices that shed alternately from each side of the cylinder, with the vortices staggered as two columnar arrays^{6,10}. For Reynolds numbers of 40 – 100,000 in which many fishes swim, the Strouhal number (St) for cylinders is 0.2, where f is the vortex shedding frequency, d is the diameter of the cylinder, and U is the nominal flow velocity.

$$St = \frac{fd}{U} \quad (1)$$

The spacing of the vortices, or wake wavelength (λ) can be calculated from the flow velocity divided by the vortex shedding frequency.

$$\lambda = U/f \quad (2)$$

This enables experimenters the ability to control the frequency and spacing of vortices by altering the flow speed and cylinder size, and has provided a unique opportunity to study how fish behave in an unsteady, periodic environment.

Previous studies revealed that fishes adopt novel body kinematics behind a cylinder, termed the Kármán gait. Kármán gaiting can save energy for station holding fishes, and occurs under certain conditions of flow velocity, body length, and cylinder size^{8,11-13}. To identify

Kármán gaiting, five criteria are used: 1) the fish is holding station and not drifting upstream or downstream, 2) there is a traveling wave along the body, 3) the body displays a large lateral displacement ($> \frac{1}{2} L$), 4) the body posture adopts a long wavelength ($> 1 L$), and 5) there are no transient small-amplitude, high-frequency tail beats.

Body wave kinematics of Kármán gaiting versus freestream swimming

A travelling wave along the body can describe both freestream swimming and Kármán gaiting kinematics for subcarangiform swimming fishes. This equation, with an arbitrary initial phase (ϕ), takes the form:

$$h(x, t) = A(x) * \sin\left(\frac{2\pi}{\lambda} x - 2\pi f t + \phi\right) \quad (3)$$

where t and x denote time and position along the body, respectively. The wave initiation point varies with the locomotor mode (thunniform, carangiform, anguilliform), which is defined according to how much of the body participates in the undulatory wave¹⁴. Tail beat frequency (f) and body wavelength (λ) define the temporal and spatial periodicity of the equation. The speed of the travelling wave (V) is defined by

$$V = \lambda f \quad (4)$$

The amplitude envelope ($A(x)$) also depends on the locomotor mode. For subcarangiform swimmers such as rainbow trout and mackerel, it is described by a second order polynomial

$$A(x) = c_1 x + c_2 x^2 \quad ^{15}.$$

Whether the travelling wave is generated actively through muscular activity or passively due to flow-induced motions varies depending on the flow regime. In freestream swimming, an antero-posterior wave of red muscle activity drives the propagation of the wave¹⁶. In contrast, during Kármán gaiting undulatory waves are generated passively as a result of lateral acceleration while the fish is being buffeted from side to side by the fluid⁸. Several findings support this argument. First, muscle recordings indicate that Kármán gaiting fish activate only the anterior red axial muscles¹². Second, dead trout temporarily generate a mechanical wave similar to live fish¹⁷. Third, there is a high correlation between the lateral acceleration and tail beat amplitude of the fish.

Freestream swimming and Kármán gaiting differ in that they are separated in the parameter space; the amplitude, wavelength and frequency values of the travelling wave equation are substantially different for each behavior¹⁸. During Kármán gaiting, the wave is initiated at the body centre, which is $0.2 L$ (where L = total body length) further down the body compared to the initiation point in freestream swimming. Fourier analysis on the motions of a dead trout towed behind a cylinder shows that in a completely passive body, the wave starts at the base of the cranium similar to freestream swimming (Fig. 1). This suggests that the location of the wave initiation point during Kármán gaiting is not due to the passive fish-fluid interactions. When live fish Kármán gait they activate their anterior muscles in order to adopt a straight posture in the mid-body region; as a result this arrangement changes the location of the initiation point. In this way, the interaction between fish and fluid in the mid-body region is more critical than the posterior region. Fish appear to keep the mid-body region from bending in order to provide a local axial control surface to harness the appropriate fluid forces. In addition to

undulation, Kármán gaiting fish also exhibit substantial lateral translations and body rotations, which can constitute up to 75% of the behavior.

Body wave speed increases with flow speed

Kármán gaiting fish respond to increasing flow speed by increasing the speed of their traveling body wave. To do so, fish increase tail-beat frequency while keeping body wavelength and amplitude constant. Why does tail-beat frequency change and not body wavelength? Kármán gaiting is a flow-dominated behavior, where cylinder wake wavelength and vortex shedding frequency drives the body wavelength and tail-beat frequency. The cylinder vortex shedding frequency, but not wavelength, increases with flow speed, setting up a condition where the body wavelength is preserved across flow speed.

Experiments have shown that even a rigid foil positioned in a vortex street can generate thrust¹⁷. What, then, is the role of the traveling wave in Kármán gait? In uniform flow, the ratio of the traveling wave to the forward body speed (i.e. slip) approaches unity when swimming is efficient because more momentum is directed towards forward thrust. This concept is less useful in a vortex street environment, where the contributions of passive versus powered thrust generation are harder to differentiate. The traveling wave is not entirely passive, given that across flow velocities body wave speed is consistently 25% greater than the speed of the vortices drifting at the nominal flow speed¹⁹.

The effect of fish length on body wavelength

Fish relate to the vortex street in different ways depending on their body length. Kármán gaiting fish require cylinder-to-body length ratios that range from 1:2 to 1:4^{11,19}. The body wavelength of the fish affects its ability to properly interact with vortices to produce thrust. In

order to Kármán gait, small fish interact differently with cylinder vortices than larger fish. When small fish Kármán gait, they have a longer body wavelength than larger fish, reflecting the relatively larger size and spacing of the cylinder vortices. Hypothetically, a larger fish may be able to adopt a shorter wavelength because the body spans to interact with two successive vortices, while a smaller fish must adopt a longer wavelength because its body can only interact with one vortex. This is the opposite of what is found in freestream swimming, where body wavelength increases with fish size²⁰. As mention above, during the Kármán gait less of the body participates in the traveling wave than observed for freestream swimming. Therefore, a longer body length does not correspond to a longer body wavelength as it seems to do for freestream swimming (Fig. 4).

Regardless of body size, Kármán gaiting fish possess a body wavelength that is longer than the wake wavelength at intermediate flow speeds. This relationship seems critical to hold station and likely orients the body to create more thrust-generating interactions with passing vortices.

Probability of Kármán gaiting depends on flow speed

One of the most important factors determining how often fish prefer to Kármán gait is the nominal flow speed to which the cylinder is exposed. Figure 2 shows that the highest probability of Kármán gaiting occurs at intermediate flow speeds between 2-5 body lengths per second¹⁹. The body center of the fish is typically located 4-6 cylinder diameters downstream from the cylinder regardless of flow velocity level (Fig. 3A). This region corresponded to a velocity deficit of about 40% of the nominal velocity (Fig. 3B). At low flow velocities fish did not Kármán gait often and their motions resembled freestream swimming. This is because vortical flows must be sufficiently developed before fish can exploit them^{8,11-13}. Kinematic results

support this interpretation; at lower flow speeds the tail-beat frequency was considerably higher than the vortex shedding frequency¹⁹. The tail-beat frequency at the low flow speed was identical to that of a freestream swimming fish²⁰. Furthermore, body wavelength and tail-beat amplitude were very similar to those found in freestream swimming fish. At the highest speeds, trout do not hold station continuously and are either drawn upstream into the suction zone behind the cylinder, or ejected laterally from the vortex street. Under these higher Reynolds number flow conditions the wake can adopt complex, three-dimensional vortex dynamics such as braid vortices and other hydrodynamic instabilities²¹. Merging and pairing between initial shear layer vortices can give rise to secondary structures that contribute to irregular vortex shedding frequencies and amplitudes^{6,22}. The resulting turbulent vortex street exceeds the stabilization abilities of fishes.

Sensory feedback during the Kármán gait

What roles do vision and the lateral line play in the ability to exploit vortices in a cylinder wake? Theoretically, the hydrodynamic conditions of an oscillating wake make it possible for any foil-shaped object of the appropriate size to generate thrust passively^{23,24}. Experimental evidence shows that a dead trout towed behind a cylinder can momentarily synchronize its body kinematics to the oscillating flow of a vortex street to generate thrust^{12,17}. However, for a fish to remain in the cylinder wake for sustained periods requires sensory feedback from the visual and lateral line systems.

In general fishes rely heavily on both visual^{25,26} and hydrodynamic²⁷⁻²⁹ cues to adapt their swimming movements to their immediate environment. Kármán gait kinematics change when the lateral line is blocked, indicating that hydrodynamic feedback is used to alter motor

output accordingly in turbulent flows. The greater variability in body wavelength for trout with a blocked vs. intact lateral line underscores the importance of detecting local flow along the body in adjusting Kármán gait kinematics to maintain a favorable posture to facilitate vortex capture. In addition, trout with a blocked lateral line hold station further downstream from the cylinder than fish with an intact lateral line. These lines of evidence reiterate that a proportion of Kármán gait kinematics are under active control and are not the sole result of passive buffeting of the body by vortices. Longer body wavelength and faster wave speed suggest that Kármán gaiting is less efficient or more energetically costly without a functional lateral line. The fact that trout in the light with a blocked lateral line do not spend as much time Kármán gaiting as trout with a functional lateral line (Fig. 5) provides behavioral evidence in support of this hypothesis.

Whether altered Kármán gait kinematics reflect muscle activity and changes in energy expenditure for the individual is currently not known. When lateral line functionality is held constant (i.e. within fish with an intact or blocked lateral line), the presence or absence of light does not change Kármán gait kinematics. This provides further evidence that when trout hold station in a vortex street the lateral line, rather than vision, plays a larger role in body kinematics.

One exception occurs where vision alone can alter Kármán gait kinematics. Fish with a blocked lateral line in the dark have a greater variability in body wavelength than fish in the light. These fish seem to have more difficulty exploiting vortices, often drifting position within the vortex street, displaying “corrective” motions, or switching to traditional undulatory swimming such as seen in uniform flow. Vision allows fish to maintain a consistent position relative to the cylinder. This may minimize the exposure to flow variation and thus variation in body wavelength, since the predictability and energy of the vortices decreases with downstream distance from the cylinder.

Energetics of Kármán gaiting

The cost of Kármán gaiting can be measuring directly and non-invasively in live fishes by employing the technique of respirometry, which measures the oxygen consumed during a particular behavior. There are several regions around a cylinder that fish choose to hold station. Figure 6 illustrates that for a given flow speed, oxygen consumption during Kármán gaiting is higher than entraining near the suction region, but lower than bow waking in the front of the cylinder¹³. Kármán gaiting represents about half of the cost (47%) of swimming in the freestream away from the cylinder. When compared to freestream swimming in flow equivalent to the reduced velocity behind the cylinder (which is about 40% of the nominal flow velocity), Kármán gaiting represents about 79% of the cost¹¹. Therefore, by exploiting vortices Kármán gaiting fish used significantly less oxygen than predicted if there were only benefiting from swimming in the reduced velocity of the cylinder wake.

Future directions

Our work on the midline kinematics of Kármán gaiting, sensory biology and energetics can be used by roboticists to develop control algorithms that can move bio-inspired robots and by computational fluid dynamics modelers to simulate fluid-structure interactions. Given that the majority of the body waves during Kármán gaiting are generated passively, it is more important for a flexible robot to control its head and the anterior body than control its posterior body. If hydrodynamic forces are harnessed appropriately at the anterior body, a travelling wave is generated passively at the posterior body starting from the body centre. This represents a paradigm shift in the field of autonomous robotics locomotion which traditionally emphasize the control of the posterior body³⁰⁻³². What Kármán gaiting studies teach us is that head control is

critical for steering and improving stability in unsteady flows by counter-balancing body rotations and lateral translation, and that control functionality can be outsourced to the visco-elastic properties of the body itself.

The study of biological locomotion in unsteady flow regimes is a promising one that stands to shed light on new mechanisms of hydrodynamic propulsion. Though vortex streets generated by cylinders has proven to be a production experimental system, overall the responses of fishes to unsteady flows remains largely unexplored. Around a single cylinder, already three distinct energy-saving behaviors are observed. What if the wakes behind three-dimensional objects, arranged in aggregations, or varying in flexibility, were investigated in more species? It is apparent that the diversity of maneuvering, wake-exploitation and drag-reduction behaviors would reflect the inexhaustible number of scenarios between over 33,000 species of fishes and unsteady flow conditions. Along this vein, experiments into more natural flow conditions stand to be well rewarded. For example, investigating the behavior of fish holding station behind two cylinders in tandem, only a slightly more involved experiment than a single cylinder but closer to mimicking flows from more natural object aggregations such as large woody debris in streams, already reveals new principles of fluid-solid interactions and wake exploitation that could not be predicted³³. Another promising topic is the investigation of how fishes navigate waves in the surf zone during foraging. With the application of Digital Particle Image Velocimetry, high speed videography and physiological techniques such as respirometry and electromyography, new insights into the mechanisms of fish locomotion are now more accessible to marine technology applications.

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Acknowledgements

255 We would like to thank Masashige Taguchi, Melanie Haehnel-Taguchi, and William Stewart for

256 helpful discussions and Melissa Ard, Maxine Floyd, and Katherine DeCesare for fish care.

257 Support was provided by NIH 1RO1DC010809-01 and NSF IOS-1257150 to J.C.L.

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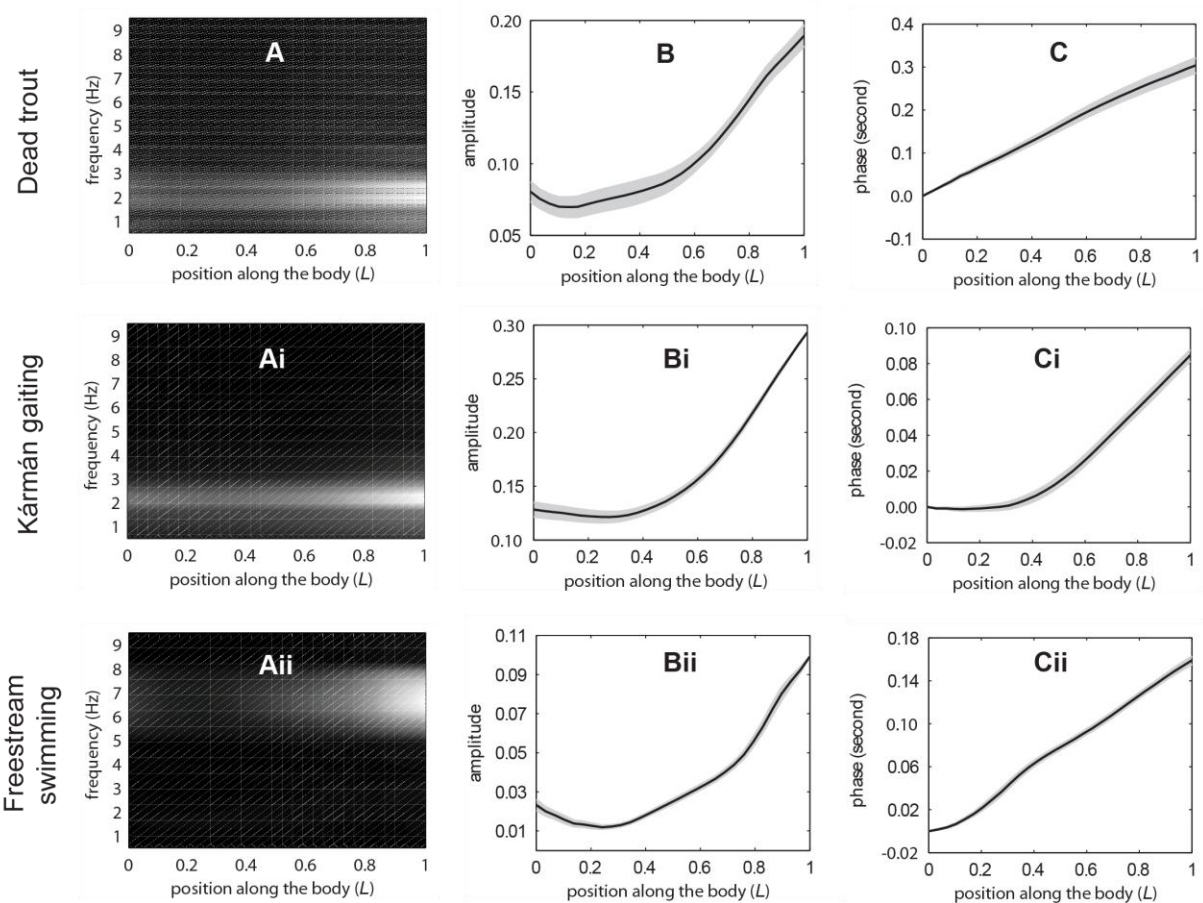
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Figures

261 Fig. 1

FIG 1

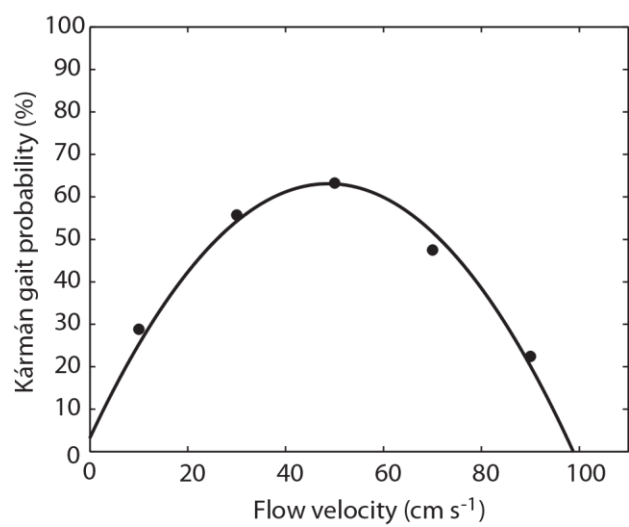


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264 Fig. 2

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Fig. 3

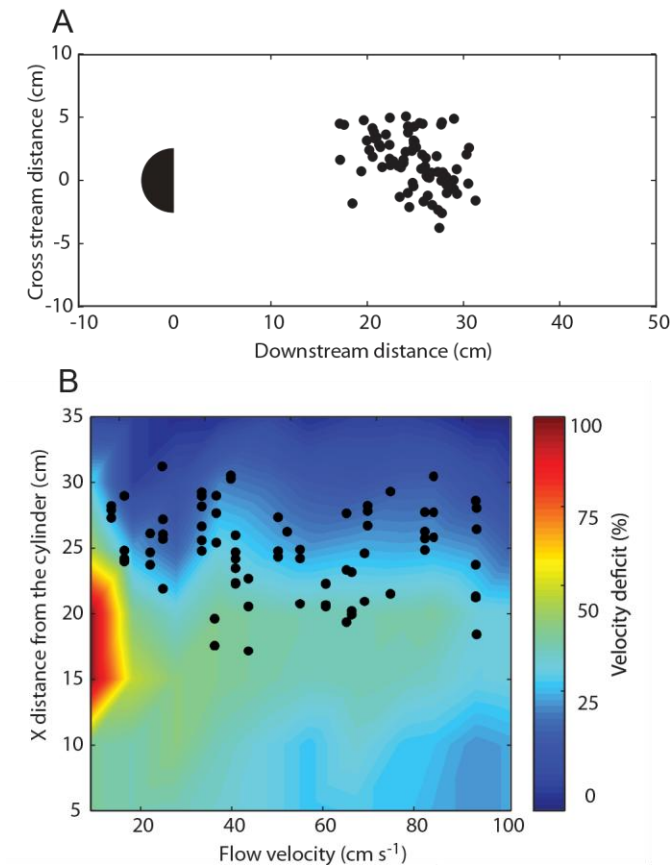
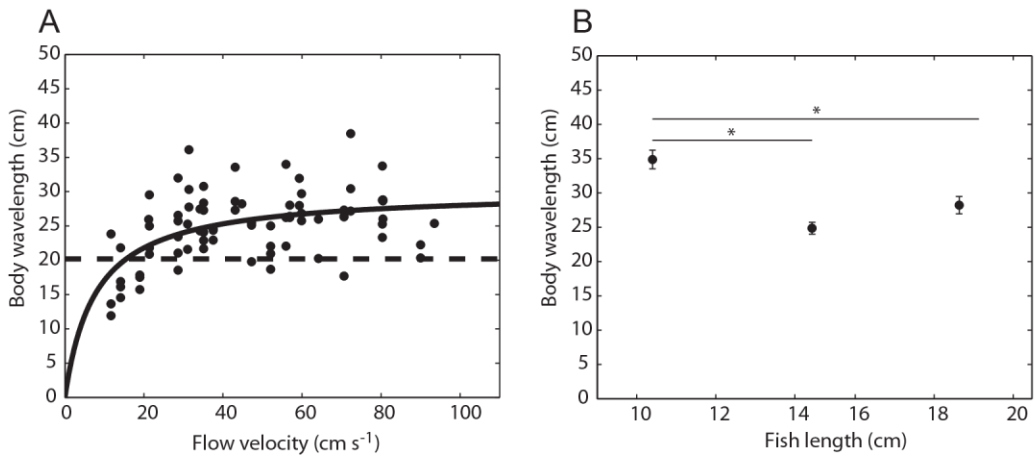
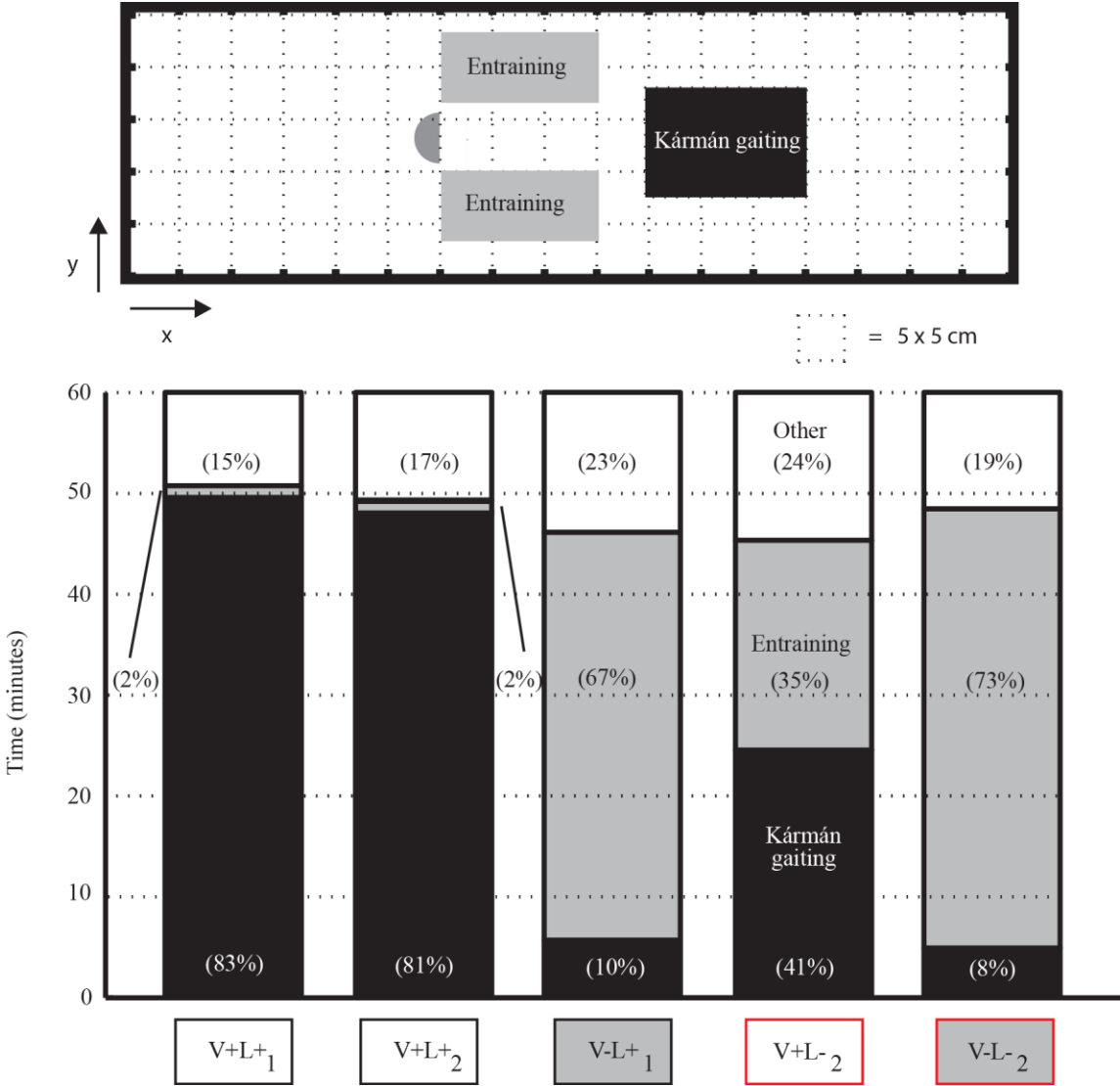


Fig. 4



286 Fig. 5

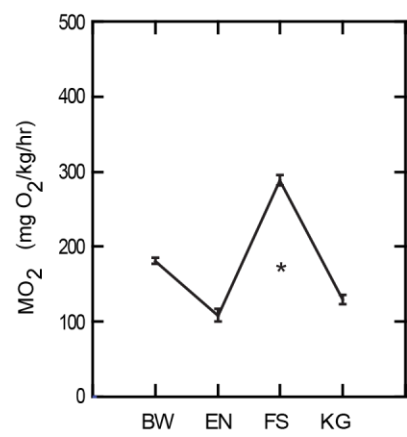


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289 Fig. 6

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Figure Legends

Fig. 1. Fourier analysis of a dead trout midline kinematics while in the vortex street ($L = 17.8$ cm, flow speed = 57 cm s^{-1} and cylinder diameter = 5 cm ¹⁷). (A) Normalized frequency spectrum (black = frequency with smallest lateral amplitude and white = largest amplitude) revealed that the dominant frequency is $2.20 \pm 0.10 \text{ Hz}$, similar to a live Kármán gaiting trout (A_i). (B) Mean amplitude curve (solid line) across 6 tail beat cycles (gray shaded area shows \pm standard error of the mean) indicated that body amplitudes of dead trout were smaller than those of live trout (B_i). (C) Increasing phase lag from head to tail in the mean phase curve (solid line, gray shaded area shows \pm standard error of the mean) indicated that the travelling wave along the body was initiated more anteriorly than in a live trout (C_i). This suggests that live fish actively control the anterior body to prevent wave formation. (A_{ii}) Normalized frequency spectrum shows both freestream swimming and Kármán gaiting fish ($L = 10.0 \pm 0.3 \text{ cm}$) at 4.5 L s^{-1} exhibited periodic lateral oscillations, where the dominant frequency was $6.6 \pm 0.1 \text{ Hz}$ and $2.2 \pm 0.05 \text{ Hz}$, respectively. (B_{ii}) Mean amplitude curves (solid line) at dominant frequency (gray shaded area shows \pm standard error of the mean). In both behaviours, the amplitude of lateral oscillations was smallest at the mid-body region and increased gradually towards tail. During Kármán gaiting, body amplitudes at all locations were larger than during freestream swimming. (C_{ii}) Mean phase curves (solid line) at dominant frequency (gray shaded area shows \pm standard error of the mean). A travelling wave was evident for both behaviours. In Kármán gaiting, the wave started at the body centre ($0.4 L$), which was about $0.2 L$ posterior to the starting point of freestream swimming fish. In both behaviours, the wave speed was constant along the posterior body ($\sim 60 \text{ cm s}^{-1}$ for freestream swimming and $\sim 75 \text{ cm s}^{-1}$ for Kármán gaiting fish). The freestream

swimming amplitude and phase curves of trout are very similar to those of saithe and mackerel presented in ¹⁵.

Fig. 2. The probability of Kármán gaiting changes with flow speed. Fish Kármán gait the most at intermediate flow speeds ($\sim 30 - 70 \text{ cm s}^{-1}$ for trout with total body length of $15.7 \pm 0.8 \text{ cm}$) and the least at extreme speeds. Videos were binned into 5 flow speed categories, where each category consisted of a minimum of 50 videos from at least 5 different fish.

Fig. 3. (A) Location of the body centre (BC, black circles) of the body relative to the D-cylinder for all trials. The x and y axes show the downstream and lateral position, respectively, where 0 corresponds to the cylinder axis. (B) Downstream position of the BC relative to the cylinder as flow velocity increases. The BC positions are superimposed on a heat map illustrating the magnitude of the velocity deficit behind the cylinder as a percentage of the freestream velocity, where red represents the greatest relative flow reduction. The location of greatest flow reduction remains in a consistent region downstream of the cylinder across most flow speeds. Note that this plot does not distinguish the reversal in flow direction that is established in the suction region directly behind the cylinder. At the lowest speed, flow reduction can equate to no flow (100% reduction), whereas at higher speeds the largest flow reduction still results in some flow magnitude.

Fig. 4. Body wavelength across speed and body size. (A) Body wavelength (solid line) starts lower than the cylinder wake wavelength (dashed line) and then rises above as flow speed increases ($r^2 = 0.28$, $n = 9$ fish). At the lowest swimming speeds, the absence of a strong vortex

street likely requires use of a shorter body wave similar to freestream swimming fish (see text).

(B) At a flow speed of $\sim 50 \text{ cm s}^{-1}$, smaller fish have a longer body wavelength than larger fish ($p < 0.05$, $n = 15$ fish). Values shown are the mean \pm S.E.M.

Fig. 5. Regions around a cylinder in flow that trout will either entrain or Kármán gait (defined as two rectangular regions on either side of the cylinder, $7 \times 15 \text{ cm}$, or a single rectangle centered along the midline of the cylinder wake, $10 \times 15 \text{ cm}$, respectively). In the light, fish prefer to Kármán gait in the vortex street downstream from the cylinder (black fill) for the majority of the time during a 60-minute experiment, especially when the lateral line is intact ($V+L+1$). Values for fish in the light with an intact lateral line exposed to the cylinder for two consecutive days ($V+L+2$) are almost identical to those exposed for one day ($V+L+1$), indicating that previous experience in the flow tank does not alter the preference to Kármán gait. In contrast to experiments performed in the light, fish in the dark do not spend much time in the vortex street regardless of lateral line functionality ($V-L+1$ or $V-L-2$), preferring to entrain (gray fill) just downstream and to the side of the cylinder. The time that fish spent exploring other regions of the flow tank (white) is similar across treatments.

Fig. 6. Statistical comparison of MO_2 values between Kármán gaiting (KG) and other behaviors at 3.5 L s^{-1} . Compared to other behaviors at 3.5 L s^{-1} , Kármán gaiting requires significantly less oxygen than swimming in the free stream (FS, 47%) and bow waking (BW, 73%), but requires more oxygen than entraining (EN, 116%). Kármán gaiting fish use less oxygen (79%) compared to fish swimming in the free stream at 1.8 L s^{-1} (asterisk). Values are reported as the mean \pm the standard error.

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